A simulation study of the determinants of adaptation of an invasive species.

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Adaptation is considered as a key process determining the ability of introduced species to become invasive. There have been few simulation studies based on explicit genetic models of evolution to study the factors influencing adaptation after introduction [1]. Furthermore for the sake of simplicity and generality, analytical models of evolution are often limited to either sexual or asexual populations in a mutation/drift equilibrium. These models are not relevant to a large class of invasive species (e.g., fungal plant pathogens) because they exhibit rapid expansion dynamics (non-equilibrium) and are capable of both modes of reproduction.

We develop a demogenetic model of species introduction using an improved version of *quantiNemo* [2] : a given rate of asexuality can be set and a species can be either haploid or diploid. We simulate the following scenario: some individuals are introduced from a source environment to a new environment with a different adaptive landscape (**Figure 1**). A quantitative trait coded by few loci can evolve on this adaptive landscape thanks to mutation, selective pressure and genetic drift. Using this model, we show how the population expansion dynamic of the introduced population is affected by the rate of asexuality, mutation parameters and distance between source and sink optimum.

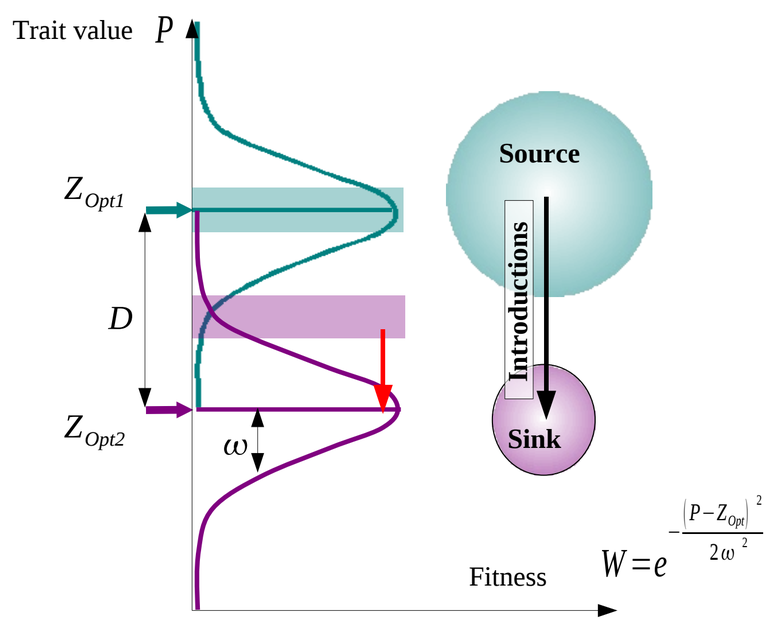

Figure 1 : Simulated scenario : A source population in selection-mutation-drift equilibrium sends migrants into a sink population. Sink and source population have a different optimum. The immigrants (red rectangle) need to adapt to their new environment (red arrow).

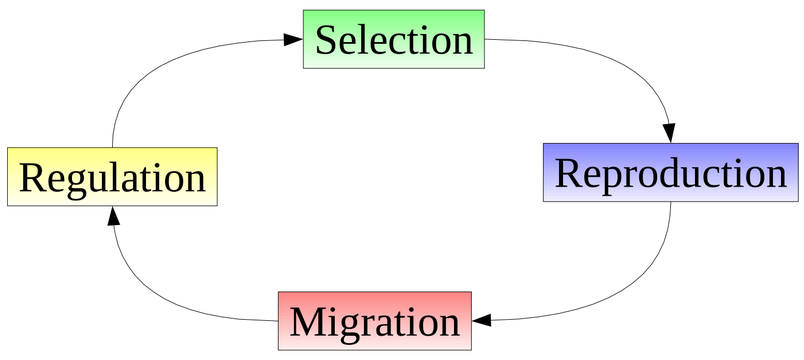

Figure 2 : Life cycle events of individuals in *quantiNemo*.

Fixed parameters	Value
Number of loci	10
Strength of selection (ω)	1
Carrying capacity of source	1000 ind
Carrying capacity of sink	750 ind
Burn-in phase	1000 gen
Simulation duration	500 gen
Fecundity	5 ind.gen^{-1}

Varying parameters	Values
Environmental variance	{0, 1}
Mutation rate	{10^{-3}, 10^{-4}} locus^{-}1.gen^{-1}
Mutation effect variance	{0.01, 0.05}
Distance between optimum (D)	{2.4, 2.8}
Asexuality rate	[0, 1]
Migration rate	{0.001, 0.005, 0.01} ind.gen^{-1}

Table 1 : List of fixed and varying parameters of the model. The burn-in phase is a time to allow the source population to reach mutation-genetic-drift equilibrium.

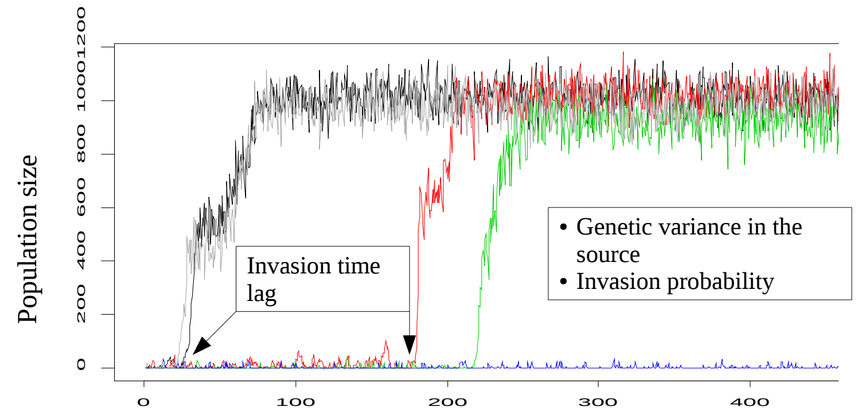

Figure 3 : 5 simulation examples of the population dynamic in the sink and measured characteristics.

Explained variable	Explanatory variable: Genetic Variance in the source	Mutation rate	Variance of mutation effects	Optimum	Asexuality rate	Explained Variance
Invasion probability		74.5	54	100	**40.6**	0.26
Invasion time lag		58.6	11.5	100	**12.9**	0.32
Genetic variance in the source		100	34.2		**16.6**	0.81
Invasion probability	**60.3**	3.17	6.6	100	43.8	0.57
Invasion time lag	**40.4**	1.6	1.7	100	0.48	0.34

Table 2 : ANOVA results. Each line corresponds to a fitted linear model. The last column gives the proportion of variance explained by the model and values in each cell give the F statistic standardised by a factor so that the highest F value is 100 after standardisation.

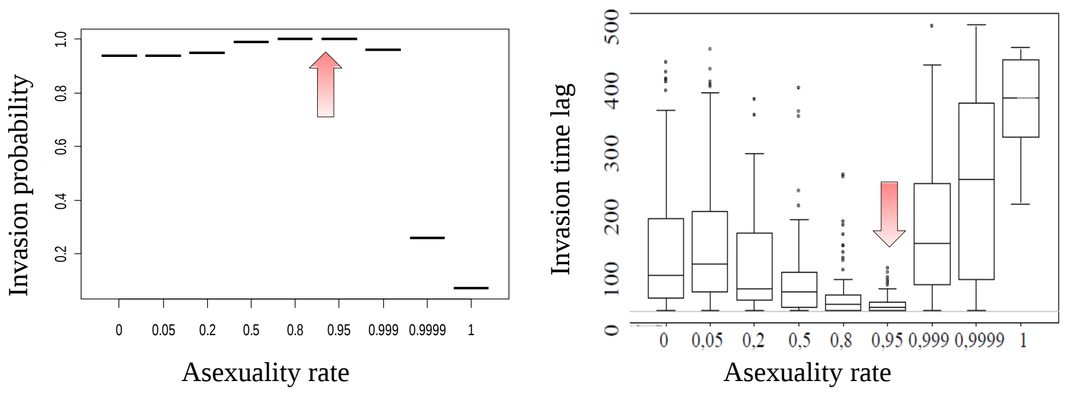

Figure 4 : Effect of asexuality rate on invasion probability and time lag.

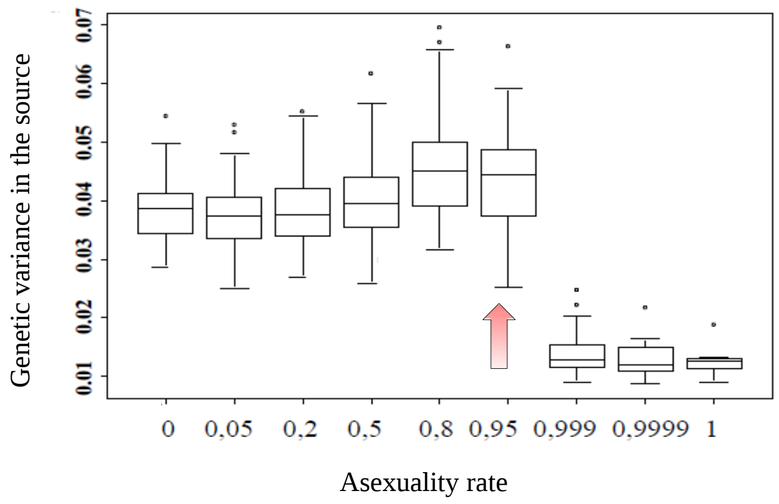

Figure 5 : Effect of asexuality rate on genetic variance in the source population.

Differences of optimum between the source and the sink populations and mutation parameters (mutation rate and variance of mutation effect) are the main factors influencing the success of an invasion (**Table 2**). Nevertheless, asexuality rate has a substantial effect on invasion dynamic. **Figure 4** shows that an optimum of invasion probability and time lag is reached for partially asexual species with a high rate of asexuality (~ 95% ⇨). This can be explained by the influence of asexuality rate on genetic variance in the source population (**Figure 5**). We hypothesize that a high asexuality rate allows a source population to retain a higher proportion of mutations because of a less efficient background selection (Hill-Robertson effect). This increases the genetic variance in the source that can be transmitted to the sink through migration. Thus, evolutionary potential and invasive capacity of immigrants are improved under these reproductive conditions.

References :

[1] Holt, R. D., Gomulkiewicz, R. & Barfield, M. 2003. The phenomology of niche evolution via quantitive traits in a 'black-hole' sink. Proceedings of the Royal Society of London Series B-Biological Sciences 270: 215-224.
[2] Neuenschwander, S., Hospital, F., Guillaume, F. & Goudet, J. 2008. quantiNemo: an individual-based program to simulate quantitative traits with explicit genetic architecture in a dynamic metapopulation. Bioinformatics 24: 1552-1553.